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## **Internal tides drive nutrient fluxes into the deep chlorophyll maximum over mid-ocean ridges**

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### **Key Points:**

- Internal tides provide a ten-fold increase in diapycnal nitrate fluxes to the deep chlorophyll maximum over the Mid-Atlantic Ridge
- Diapycnal nitrate fluxes increase by a factor of eight between neap and spring tides
- Global tidal modelling experiments reveal that spring-neap enhancement in diapycnal nitrate fluxes is widespread over ridges and seamounts

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## Abstract

Diapycnal mixing of nutrients from the thermocline to the surface sunlit ocean is thought to be relatively weak in the world's subtropical gyres as energy inputs from winds are generally low. The interaction of internal tides with rough topography enhances diapycnal mixing, yet the role of tidally-induced diapycnal mixing in sustaining nutrient supply to the surface subtropical ocean remains relatively unexplored. During a field campaign in the North Atlantic subtropical gyre, we tested whether tidal interactions with topography enhances diapycnal nitrate fluxes in the upper ocean. We measured an order of magnitude increase in diapycnal nitrate fluxes to the deep chlorophyll maximum (DCM) over the Mid-Atlantic Ridge compared to the adjacent deep ocean. Internal tides drive this enhancement, with diapycnal nitrate supply to the DCM increasing by a factor of eight between neap and spring tides. Using a global tidal dissipation database, we find that this spring-neap enhancement in diapycnal nitrate fluxes is widespread over ridges and seamounts. Mid-ocean ridges therefore play an important role in sustaining the nutrient supply to the DCM and these findings may have important implications in a warming global ocean.

## Plain Language Summary

The subtropical gyres cover an extensive area of the global ocean and account for ~30% of carbon export to the deep ocean. The pattern of the winds induce downwelling in these gyres and lead to surface waters being relatively nutrient impoverished. Biological production in the subtropical gyres is primarily limited by the availability of nitrate, which can be increased through mixing in the underlying thermocline. Internal tides can enhance mixing in the ocean interior close to steep sloping topography; deep in the ocean interior, this mixing is a key component of ocean physics. In our field study, we reveal the mixing extending up towards the surface and measured a ten-fold increase in nitrate fluxes to phytoplankton in the surface ocean over the Mid Atlantic Ridge compared to in the surface waters in the adjacent deeper ocean. Importantly, nitrate fluxes over the ridge varied fortnightly with a six-fold increase from neap to spring tides. These inferences of enhanced mixing and nutrient supply along ridges and seamounts are relevant for the rest of the global ocean given the ubiquitous nature of the tides.

## 1 Introduction

Internal tides are viewed as a major energy source for upper-ocean mixing (Waterhouse et al., 2014, Kunze, 2017). The resulting diapycnal nutrient fluxes driven by this upper-ocean mixing are widely recognised as being important in sustaining primary productivity in the continental shelf seas (Sharples et al., 2007, Tweddle et al., 2013, Villamana et al., 2017, Rippeth and Inall 2002). In contrast, these diapycnally-driven nutrient fluxes are viewed as relatively unimportant in the open ocean. In the deep open ocean, diapycnal mixing is spatially patchy, the turbulent kinetic energy dissipation varying by one to two orders of magnitude, and with enhanced mixing extending up to 1-2 kilometres above rough topography (Waterhouse et al., 2014, Kunze et al., 2006, Polzin et al., 1997). This enhanced mixing is associated with the breaking of internal waves driven by the interaction of the internal tide and rough topography (Garrett and Kunze, 2007, Egbert and Ray, 2000, Munk and Wunsch, 1998). In the upper open ocean, diapycnal mixing is sustained by internal tides (Lefauve et al., 2015, Kunze, 2017, Lavergne et al., 2019, Hibiya and Nagasawa, 2004, Melet et al., 2016) and also the near-inertial inputs of wind energy (Whalen et al., 2018, Alford, 2012). The low inputs of wind energy into the subtropical gyres, particularly in summer months, has led to a prevailing view that the diapycnal nutrient flux to the surface ocean is relatively weak. In this study, we explore the relative importance of the internal tide in providing an enhancement in the diapycnal supply of nutrients in the upper open ocean along topographic ridges and regions of shallow bathymetry.

The diapycnal flux of a nutrient ( $N_u$ ) is the product of the vertical gradient of the tracer concentration ( $\partial N_u / \partial z$ ) and the local diapycnal diffusivity ( $K_z$ ), i.e. nutrient flux =  $-K_z (\partial N_u / \partial z)$ . The diapycnal diffusivity is estimated from the local rate of dissipation of turbulent kinetic energy and the inverse of buoyancy frequency (Osborn, 1980). Variability in  $K_z$  over the open ocean is revealed by microstructure measurements, and typically ranges from  $\sim 10^{-6}$  to  $10^{-5} \text{ m}^2 \text{ s}^{-1}$  in deep ocean basins, and up to  $10^{-4}$  to  $10^{-2} \text{ m}^2 \text{ s}^{-1}$  near ocean ridges and seamounts (Waterhouse et al., 2014, Polzin et al., 1997).

To affect nutrient fluxes and primary production, enhanced  $K_z$  from tidal energy must reach the base of the euphotic zone, where sharp nutrient gradients separate the dark nutrient-rich interior and the nutrient-deplete euphotic zone (Lewis et al., 1986, Sarmiento et al., 2004, Peligri et al., 2006, Figure S1). If either  $K_z$  and/or the nutrient gradient are increased, then the supply of ‘new’ nutrients mixed up from the ocean interior is enhanced. During summer in the subtropical ocean, nutrients become exhausted in the mixed layer and throughout the euphotic zone. As a result, a chlorophyll feature in the subtropical ocean, the deep chlorophyll maximum (DCM), emerges at the base of the euphotic zone, concomitant with the upper thermocline. Measurements from the subtropical North Pacific indicate that the DCM might be locally important, accounting for 34% of particulate nitrogen export (Letelier et al., 2004). Enhanced diapycnal mixing from the interaction of internal tides with mid ocean ridges may increase export production by augmenting the nutrient supply to the DCM.

In this paper, we determine how the internal tide drives changes in the diapycnal nitrate flux to the base of the DCM. We first present the analysis of observations from a field campaign within the North Atlantic subtropical gyre, over and adjacent to the Mid-Atlantic Ridge (Section 2), which are compared to regional wind and tide estimates (Section 3). We then employ a tidal model of energy dissipation to illustrate the larger-scale implications of the observed signal of enhanced diapycnal nutrient fluxes over complex topography (Section 4), and then discuss the wider implications of the study for subtropical gyres (Section 5).

## 2 Field Survey

### 2.1 Field measurements

This field study took place in the North Atlantic subtropical gyre between 24° to 36°N, to assess the influence of the internal tides on diapycnal nutrient fluxes over the Mid-Atlantic Ridge and the adjacent abyssal ocean (Figure 1). The sampling campaign was conducted on the RRS *James Clark Ross* during May to June 2015. The survey began in the north-western corner of the study area at spring tide and continued in a clockwise direction around the transect. Salinity, temperature and depth were measured using a CTD system (Seabird 911+) with salinity calibrated on-board with discrete samples using an Autosal 8400B salinometer (Guildline). Photosynthetically Active Radiation (PAR) from the CTD was used to calculate the euphotic layer depth, which was defined as the depth where PAR decreased to 1% of the surface value. The CTD fluorescence sensor was calibrated using a Turner Trilogy fluorometer with measurements conducted in the upper 300m.

At all stations micro-molar nutrient analysis was carried out using a four channel (nitrate, nitrite, phosphate and silicate) Bran & Luebbe AAIII segmented flow, colorimetric, auto-analyser. Certified reference materials (BU) were analysed every 2-3 runs to ensure continued precision throughout the cruise, with cruise averages within the accepted range for each nutrient and a 99% precision. Two internal standards covering a wide range of concentrations for nitrate, phosphate and silicate were analysed in each run.

Full water column profiles of turbulent dissipation and diffusivity were made using a free falling Vertical Microstructure Profiler (VMP6000, Rockland Scientific). In addition to spatial coverage around the cruise track, the resolution of tidal semi-diurnal variability was recorded by carrying out continuous profiling of the upper 1000 m (sometimes down to 1800 m) using a VMP2000 at two stations, one in the north-eastern (on ridge) and one in the north-western (off ridge) corner of the transect (Figure 1). At the on ridge tidal station, continuous sampling for 25 hours and 15 hours was carried out during spring and neap tides respectively, while at the off ridge station continuous sampling was carried out for 20 hours during a spring tide. The microstructure for the temperature and velocity shear were measured on the length scales of dissipation of turbulent flows, typically a few millimetres to tens of centimetres. The rates of the dissipation of turbulent kinetic energy ( $\epsilon$  ( $\text{m}^2 \text{s}^{-3}$ )) were estimated following the methods by Oakey (1982).

Diapycnal diffusivity,  $K_z$  ( $\text{m}^2 \text{s}^{-1}$ ) was calculated from

$$(1) \quad K_z = \Gamma \frac{\epsilon}{N^2} (\text{m}^2 \text{s}^{-1})$$

where  $N$  is the buoyancy frequency ( $\text{s}^{-1}$ ) and  $\Gamma$  is the mixing efficiency (Figure 2). Based on the typical conditions measured in the upper 500 metres during the cruise,  $\Gamma$  was taken to be constant at 0.2 (Gregg et al., 2018 and references therein).

### 2.2 Enhanced Upper Ocean mixing over the Mid-Atlantic Ridge

We designed a field experiment to test the hypothesis that the generation of internal tides over mid ocean ridges and resulting internal wave breaking can drive increased diapycnal mixing and enhance nitrate fluxes to the base of the DCM. The field programme provided

estimates of diapycnal diffusivity  $K_z$  and nutrient fluxes over the Mid-Atlantic Ridge and adjacent abyssal ocean (Figure 1).

There is a consistent enhancement in the turbulent kinetic energy dissipation over the upper 2000 m above the ridge relative to in the deeper basin (Figure 2a, blue versus red). Combining with the buoyancy frequency, there is then a systematic enhancement in the diapycnal mixing over the ridge by typically one order of magnitude over much of the water column (Figure 2b, c).

Now focusing on the upper 500 m, turbulent microstructure measurements revealed dissipation rates over the ridge that were enhanced by a factor of between 4 and 10 compared to off ridge (Figure 1a). The associated  $K_z$  is similarly enhanced, extending to the upper ocean and reaching the base of the DCM, where there was an increase from an average of  $2.3 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$  in the basin to  $1.3 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$  over the ridge (Figure 3a, Table 1). Spatial variability in  $K_z$  along the ridge section was partially due to the gradually deepening ridge crest towards the south (Figure 1 and 3), but was associated also with the spring-neap cycle and regions where the rough seafloor generates energetic high-mode internal waves that are prone to breaking and increasing  $K_z$  (Falahat et al., 2014, Vic et al., 2018).

Diapycnal nitrate fluxes to the DCM were determined by  $K_z$  combined with vertical nitrate gradients at the base of the DCM (Sharples et al., 2007; Omand and Mahadevan, 2015). There is a nitrate supply to the DCM whenever there is a convergence in the diapycnal nitrate flux. As nitrate becomes depleted above the DCM and the vertical nitrate gradient becomes small, then a diapycnal nitrate flux at the base of the DCM automatically corresponds to a diapycnal supply of nitrate. Enhanced diapycnal mixing increases the diapycnal nitrate flux at the base of the DCM and so increases the nitrate supply to the DCM, which can either increase nitrate in the DCM or possibly sustain more phytoplankton growth.

There is an order of magnitude increase in the diapycnal nitrate flux between the off and on ridge sites (Figure 3d and Table 1). This ridge-enhanced diapycnal nitrate supply arises from both the increase in  $K_z$  and the increase in the vertical nitrate gradient on the ridge (Table 1). There are stronger vertical gradients at the base of the DCM over the ridge compared to off ridge for all macronutrients (N, P, Si), further supporting the view of increased diapycnal mixing.

### 2.3 Internal tides and mixing over spring and neap cycles

The enhanced diapycnal mixing over the ridge compared to the abyssal ocean is likely to be generated by tidal interaction with rough topography (Toole, 2007, St Laurent and Garrett, 2002). In order to test this viewpoint, we conducted three time-series stations with a turbulent microstructure profiler, each station covering 1 - 2 semi-diurnal tidal cycles (Figure 4). Turbulent diffusivity in the base of the DCM on the ridge increased from  $1.3 \times 10^{-5}$  to  $9.3 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$  from neap to spring tides (Figure 4a, b), and was three times higher at neap tides and 20 times higher at spring tides than spring tide at the off ridge site (Figure 4 and 5b). The enhanced tidal mixing and associated  $K_z$  on the ridge has a marked fortnightly spring-neap periodicity. This fortnightly variation in  $K_z$  produced by the barotropic tide flowing over rough topography has been discussed in previous field studies (Toole, 2007).

Observations of diapycnal diffusivity and vertical nitrate gradients over the ridge reveal an increase in diapycnal nitrate fluxes to the DCM from 0.03 to  $0.27 \text{ mol N m}^{-2} \text{ yr}^{-1}$  from neap to spring tides (Figure 5b-d). The diapycnal nitrate flux becomes small in the surface mixed



layer due to the depletion of mixed-layer nitrate. The diapycnal nitrate flux reaches a sub-surface maximum at depths of around 100m off the ridge and during the neap tide on the ridge, but reaches a sub-surface maximum at 60m during the spring tide on the ridge. This depth-structure of the diapycnal nitrate flux drives a supply of nitrate at depths between 50m to 100m during the spring tide on the ridge, and a loss of nitrate from depth between 100m to 150m (Figure 5e, red line). There is a similar, but weaker in magnitude, structure for the nitrate supply associated with the neap tide on the ridge and the spring tide off the ridge (Figure 5e, yellow and blue lines). The variability in the diapycnal nitrate supply over a spring-neap cycle also alters the depth of the chlorophyll maximum, with the DCM shallowing from 100m to 50m from neap to spring tides on the ridge, coinciding with the maximal nitrate supply (Figure 5e, f).

The on-ridge nitrate supply to the DCM at spring tide was 67 times higher than the off-ridge flux (Table 1). The strength of the diapycnic mixing on the ridge is related to both the spatial variability associated with seabed topography and the temporal variability driven by the spring-neap tidal cycle. In addition, nitrate fluxes over the ridge (Figure 3) vary according to changes in the vertical gradient in the nutrients and hotspots of expected mixing where there may be regions of super-critical seabed slope.

### 3 The contribution of tides and winds to diapycnal nitrate fluxes

During our summer survey, the surface mixed layer is relatively thin, only reaching depths of 20 to 50 m, and the layer of peak chlorophyll and the lower limb of the DCM lies within the seasonal pycnocline, at depths of  $102 \pm 35$  m and  $165 \pm 44$  m respectively. There are two primary candidates to drive the diapycnal mixing at the base of the DCM: wave breaking due to winds or tides.

To determine the impact of the winds relative to the tides over the relevant depth ranges, the kinetic energy content is evaluated at near-inertial and semidiurnal frequencies in the upper 500m, which are taken to be representative of the dominant wind and M2 tidal frequencies respectively. The time mean and standard deviation of the velocities were evaluated from mooring ADCP data at the on-ridge site (Figure 5a). Horizontal velocity fields were filtered at the M2 and inertial frequencies using a bandpass fourth-order Butterworth filter in the bandwidth  $[\frac{\omega}{c}, c\omega]$  with  $c=1.25$  and  $\omega=1.4 \times 10^{-4} \text{ s}^{-1}$  for the M2 frequency (Alford, 2003) and  $\omega=0.86 \times 10^{-4} \text{ s}^{-1}$  for the inertial frequency. The kinetic energy per unit volume,  $0.5\rho_0(u'^2 + v'^2)$ , is evaluated from the filtered velocities  $u'$ ,  $v'$  and  $\rho_0=1025 \text{ kg m}^{-3}$ . Note, however, that the near-inertial kinetic energy reservoir does not necessarily feed local turbulence. The wind contribution from the near-inertial energy input is mainly confined close to the surface in the upper 50m, while the semi-diurnal tidal energy input dominates over the wind energy input below the mixed layer, reaching a factor of two larger within the DCM (Figure 5d).

To provide an additional context, we compared the tidal and wind energy inputs over the mid-Atlantic ridge region (Figure 6). Specifically, we used the fraction of tidal energy conversion that goes into high-mode ( $>4$ ) internal tides,  $E_t$ , from Vic et al (2019). Vic et al (2019) showed that this is an accurate estimate of the tidally-driven 'near-field' energy dissipation. 'Near-field' here refers to the fraction of the tidal energy input that dissipates into local turbulence (MacKinnon et al, 2017).  $E_t$  is enhanced over the ridge, where the tidal currents are stronger and the seafloor topography is rougher (Figure 6c) (Vic et al., 2018);

this locally-generated tidal component is also referred to as the near-field dissipation (MacKinnon et al., 2017). The wind energy flux is the total wind energy input to near-inertial motions in summer ( $E_{w-s}$ ) and in winter ( $E_{w-w}$ ) from Whalen et al (2018). The near-inertial motions lead to shear across the transition layer, and this process is a major component of mixing in the upper ocean (Alford et al., 2016).

The summer wind energy input is relatively modest due to light wind conditions but much stronger in winter,  $E_{w-w}$ , due to enhanced atmospheric storm activity (Figure 6a, b). The wind energy flux is enhanced in the north-western corner of the area (Figure 6a, b), also coinciding with enhanced ocean mesoscale eddy activity (Whalen et al. 2018). Over the ridge, the tidal energy flux dominates the wind energy flux in summer, with an input of 6.80 GW compared to 2.94 GW (Figure 6d, f, evaluated over hatch-free area). However, the tidal and wind energy fluxes become comparable in winter (Figure 6e, f), with a wind energy flux of 6.83 GW. Tidal and wind-driven processes that lead to mixing are not totally independent. Tidal and near-inertial waves can interact non-linearly and cascade down to dissipation (Cuyppers et al 2017). Nonetheless, at the time of the measurements, light-wind conditions did not favour those interactions.

In conclusion, the diapycnal mixing driving nutrient fluxes for the DCM are likely to be sustained by the tides rather than winds due to (i) the kinetic energy content being dominated by semi-diurnal frequencies below the mixed layer (Figure 5d); (ii) there being a spring-neap modulation in the diapycnal diffusivity (Figure 4) and (iii) the summer input of kinetic energy over the entire water column being dominated by the tides rather than the winds (Figure 6d, f). Therefore in summer months, tides are likely to dominate the regional nutrient supply in the North Atlantic subtropical gyre.

#### 4 Basin-scale perspectives from a global tidal dissipation model

The results from our field study reveal the importance of internal tides in driving nutrient fluxes to the DCM over the mid-Atlantic ridge. The results imply that in regions of the oligotrophic gyres close to ridges and seamounts, nutrient fluxes are likely to be augmented by internal tides and undergo a fortnightly fluctuation. To test whether the inferences from our field study are significant on larger scales, we employ a tidal model (TPXO8) (Egbert and Erofeeva, 2002) and a climatology of nutrient distributions (WOA v2) (Boyer et al., 2013) to investigate how variable tidally-driven  $K_z$  affects the magnitude and distribution of nutrient supply in the subtropics.

The tidal dissipation,  $D$ , for the global diffusivity fields was computed using the TPXO8 data set (available from [http://volkov.oce.orst.edu/tides/tpxo8\\_atlas.html](http://volkov.oce.orst.edu/tides/tpxo8_atlas.html)), following Egbert and Ray, (2001):

$$(2) \quad D = W - \nabla \cdot P ,$$

where,  $W$  is the work done by the tide-generating force and  $P$  is the horizontal energy flux vector, which are calculated from

$$(3) \quad W = g\rho\langle \mathbf{U} \cdot \nabla(\eta_{EQ} + \eta_{SAL}) \rangle ,$$

$$(4) \quad P = g\rho\langle \mathbf{U}\eta \rangle ,$$



where the angular brackets mark time averages over a tidal period,  $g$  is gravity,  $\rho$  is sea-water density,  $\mathbf{U}$  is the tidal transport vector,  $\eta$  is the tidal amplitude, and  $\eta_{\text{sal}}$  and  $\eta_{\text{EQ}}$  are the self-attraction and loading amplitude and the equilibrium tide, respectively.

The tidal dissipation energy was then used to compute a vertical diffusivity from a modified version of equation (1),

$$(5) \quad K_z = \Gamma q \frac{D(x,y)F(x,y,z)}{\rho N^2},$$

Where  $q$  is the dissipation efficiency (the fraction of converted energy that dissipates within the local water column), and  $F$  is a function that describes the vertical distribution of the converted energy. The dissipation efficiency,  $q$ , is assumed following Vic et al, (2019) to be  $q=0.8$  in the Atlantic and  $0.5$  in the Pacific; in practice, similar vertical diffusivity profiles are obtained in a sensitivity test using  $q=0.3$  and adding a small constant vertical diffusivity. For the vertical distribution of the converted energy, following St Laurent et al. (2002), Schmittner and Egbert (2012) and Melet et al. (2013), we divide the energy in half and assume that one half experiences bottom-enhanced dissipation and the other half is dissipated at a rate proportional to  $N^2$ . The bottom intensified half of the energy decays vertically with an e-folding scale of 500m and thus provides only a small amount to the diffusivity at 500m (st Laurent et al, 2002, Polzin, 2006). The other half of the local energy dissipation scales proportionally with  $N^2$ , such that that  $F(x, y, z) = N^2(x, y, z) / \int N^2(x, y, z) dz$ , integrated from the surface to the seafloor (e.g., Gregg 1989, Kunze 2017). These assumptions for the energy dissipation leads to dissipation occurring within the thermocline and near the bed, consistent with our observations.

Tidal dissipation estimates over spring and neap tides are used to calculate the fortnightly variation in vertically integrated tidal dissipation. The associated vertical diffusivity is computed by distributing the dissipated energy over depth assuming that the vertical distribution of dissipation is proportional to the squared buoyancy frequency and the local breaking of internal tides. We estimate an upper ocean diapycnal diffusivity  $K_z$  over the Atlantic and Pacific subtropical gyres (100-500 m) associated with internal tide generation ( $K_{z\text{-tide}}$ ), which is in accord with the diffusivity profiles measured from the Mid-Atlantic Ridge field study (Figure 7).

The diapycnal diffusivity estimated from the internal tide  $K_{z\text{-tide}}$  is typically four times larger over ridges and seamounts compared to over the smooth, deep basins (ridges= <4000 m, deep basins= >4000 m). The effects of neap and spring tides are evident, with the area-averages fluctuating by more than a factor of two over a fortnightly cycle. The tidally-generated diapycnal nitrate fluxes are estimated by combining this diapycnal diffusivity  $K_{z\text{-tide}}$  with the maximum vertical nitrate gradient in the upper 500 m of each grid using data from WOA13v2 (Figure 8a).

Over large swathes of the subtropical gyres where the influence of tidal-driven mixing is negligible, diapycnal nitrate fluxes are very low ( $0.01 \pm 0.001 \text{ mol N m}^{-2} \text{ yr}^{-1}$ ). In contrast, over regions of ridge systems, area-averaged annual diapycnal nitrate fluxes are  $0.05 \pm 0.01 \text{ mol N m}^{-2} \text{ yr}^{-1}$ . Area integrated fluxes over ridges and the deep ocean reveal that ridge

systems which account for only 29% of the study region provide 62% of the tidally-generated nitrate flux.

Basin-wide diapycnal nitrate flux estimates over the Atlantic Ocean from internal tides are  $\sim 0.03 \text{ mol N m}^{-2} \text{ yr}^{-1}$ , accounting for approximately one half of current total estimates of diffusive supply from inertial shear and internal tides ( $\sim 0.05 \text{ mol N m}^{-2} \text{ yr}^{-1}$ , Williams and Follows, 2011). The diapycnal nitrate fluxes generated by internal tides also importantly create a fortnightly fluctuation in nutrient supply over ridge and seamount regions. The tidal variability in the Atlantic and Pacific subtropical gyres suggest basin-scale averaged diapycnal nitrate fluxes during spring tides are typically 2-3 times greater than during neap tides.

## 5. Wider implications for the subtropical gyres

The role of the internal tide in providing enhanced mixing and diapycnal nitrate fluxes to the surface ocean is now discussed in terms of the possible effect on export production and community structure. Over annual or longer timescales, nutrient supply and export production are expected to balance. Thus, estimates of export production in the subtropical ocean require a nitrogen supply term of approximately  $0.5\text{-}0.9 \text{ mol N m}^{-2} \text{ yr}^{-1}$  (Jenkins 1982, Jenkins and Doney, 2003). This is validated by geochemical estimates of the physical supply of nitrate to the euphotic zone of the subtropical North Atlantic which range between  $0.7\text{-}0.8 \text{ mol N m}^{-2} \text{ yr}^{-1}$  (Jenkins and Doney, 2003, Stanley et al., 2015). These estimates exclude the biological sources of nitrogen from nitrogen fixation or zooplankton migration which would increase the supply term further (Mahaffey et al., 2005, Tuerena et al., 2015, Bianchi et al., 2013).

Current estimates of spatially averaged diapycnal nitrate supply to the gyres range from  $0.002$  to  $0.055 \text{ mol N m}^{-2} \text{ yr}^{-1}$  (Lewis et al., 1986, Dietze et al., 2004, Fernandez-Castro et al., 2015, Mourino-Carballido et al., 2011, Painter et al., 2013), and thus only provide up to 5-10% of the necessary nitrogen. The remaining required nitrogen may be supplied from a variety of mechanisms (Williams and Follows, 2011): from (i) the atmosphere, via surface deposition or nitrogen fixation (Gruber and Sarmiento, 1997); (ii) a vertical redistribution of nutrients by convection (Williams et al., 2000), additional diapycnal mixing from salt fingering (Oschlies et al., 2003), and mesoscale eddy upwelling (McGillicuddy et al., 1998, Oschlies, 2002); and (iii) a horizontal redistribution of nutrients by horizontal Ekman transfer (Williams and Follows, 1998, Palter et al., 2005), transfer of dissolved organic nitrogen (Roussenov et al., 2006, Williams et al., 2011), and horizontal eddy transfer of nutrients (Lee and Williams, 2000).

The results from this study provide an updated perspective on the diapycnal nutrient supply within the subtropical ocean. The general view is that winds are the primary factor determining nutrient fluxes in the upper ocean. There is a low impact of wind-induced mixing in the central parts of the subtropical gyres, leading to a low diapycnal nutrient supply. Local wind and buoyancy forcing in the subtropics create an environment where there is convection and entrainment in winter, and stratification and nutrient limitation in summer. In contrast, tidally-induced mixing increases over ridges and seamounts and is not expected to be affected by seasons, but instead is modulated on a fortnightly cycle with the spring and neap tides.

These findings suggest a previously overlooked significance for the DCM over the stratified ocean. This ubiquitous layer is generally viewed in the open ocean as a result of local photo-acclimation, with increases in biomass occurring only when the layer is influenced by diapycnal mixing acting on the vertical nutrient gradients (Mignot et al., 2014). Interception of the enhanced nitrate flux by phytoplankton within the DCM will lead to changes which are not detected in satellite estimates (Letelier et al., 2004). The internal tidal waves may also boost light availability for DCM phytoplankton (Evans et al., 2008). The enhanced mixing will transfer nutrients upward in the DCM to regions of more light. At the same time the waves will oscillate the DCM through the light gradient, as seen in the excursions of isotherms at the mooring site (Figure S3). In our study, isopycnals in the base of the DCM over the ridge were seen to be oscillated about their mean depth by  $\pm 10\text{m}$  at neap tides and  $\pm 20\text{m}$  at spring tides. Thus, predictable fortnightly and semi-diurnal tidal oscillations vary the light and nutrient availability over ridges, creating a changing biome.

The ecosystem implications of the tidal mixing are now considered. The upper euphotic layer in the subtropical ocean is dominated by small-celled cyanobacteria (Legendre and Rivkin, 2002). In contrast the species assemblage at the DCM is determined by the ambient nutrient and light availability (Sharples et al., 2007), and in the subtropics contains a diverse assemblage of prokaryote and eukaryote phytoplankton (McManus and Dawson, 1994). Hotspots of tidally-induced mixing increase the proportion of new nitrate supply to the DCM which may shift local community f-ratios (the ratio of primary production fueled by nitrate compared to regenerated nitrogen) (Fawcett et al., 2011).

We explored these potential changes by assuming that tidal nitrate fluxes over the oligotrophic gyres are converted to carbon following Redfield stoichiometry (C:N=106:16). The carbon fixation thus provides an estimate for new production (as supplied from the thermocline). The community f-ratio is calculated using satellite based estimates of primary production (Behrenfeld and Falkowski, 1997, Behrenfeld et al., 2006), whereby, the community f-ratio is equal to [Redfield carbon fixed by internal tidal supply of nitrogen] / [annual net primary production from satellite]. Estimated f-ratios are enhanced over ridges and seamounts across the wider subtropical ocean (Figure 8c).

The differing nitrogen uptake strategies of phytoplankton will alter the success of particular species or algal groups depending on the availability of recycled ammonium or nitrate from the underlying thermocline. For example, eukaryotes are adapted to assimilate new nitrate over ammonium in subtropical regions (Fawcett et al., 2011). In areas of low diapycnal mixing, the available fixed nitrogen is likely to be dominated by recycled nitrogen, where prokaryotes can outcompete eukaryotes for the less energy expensive source of nitrogen (Sharples et al., 2009).

Reducing nutrient and light limitation can further increase growth rates and/or shift the community size structure towards larger species such as diatoms, increasing the potential for carbon export (Maranon et al., 2015, Siegel et al., 2014). Thus, modulating light and nutrient conditions at the DCM over ridges and seamounts could have important consequences for local community structure, which may have implications for particulate carbon export (Boyd and Trull, 2007) and enhance pelagic biodiversity up into higher trophic levels (Morato et al., 2010).

## 6. Conclusions

This study explores the implications of tidally-generated diapycnal nutrient fluxes in the vast subtropical ocean gyres, where diapycnal mixing is often considered to be dominated by the wind and is relatively weak over the central parts of these gyres. Our field campaign in the North Atlantic subtropical gyre reveals that there is enhanced tidal dissipation and diapycnal mixing along the mid-Atlantic ridge, which extends over much of the water column. This enhanced mixing redistributes nutrients from the thermocline to the surface ocean, and provides an increased diapycnal flux of nutrients to the deep chlorophyll maximum. Our analyses from the field study reveal that these enhanced nutrient fluxes also have a predictable fortnightly variability, with an eight-fold increase in nitrate supply to the deep chlorophyll maximum. This enhanced mixing from the tides crucially acts over a depth range where there are available nutrients, and so sustaining phytoplankton growth in the deep chlorophyll maximum. In contrast, the mixing from winds is strongest within the surface mixed layer where there are a lack of nutrients over much of the year.

Upscaling our fieldwork by using a global tidal dissipation database, we find that this spring-neap enhancement in diapycnal nitrate fluxes is ubiquitous over regions of rough or steep sloping topography. This mechanism of tidally-enhanced mixing in sustaining nutrient supply to the upper ocean is important on a global scale where there is shallow topography, including ridges and sea mounts, given the ubiquitous nature of the tides. This enhanced diapycnal supply of nutrients over shallow topography is expected to help sustain export production and modify the local community structure, as well as potentially affect the ecosystem response to future ocean warming scenarios.

### **Acknowledgments, Samples, and Data**

All nutrient, hydrographic and mixing data from the RidgeMix cruise which are used in this study have been submitted to the British Oceanographic Data Centre and are freely available on request (<https://www.bodc.ac.uk/data/>). The data used to support the findings of this study are also available from the author upon request.

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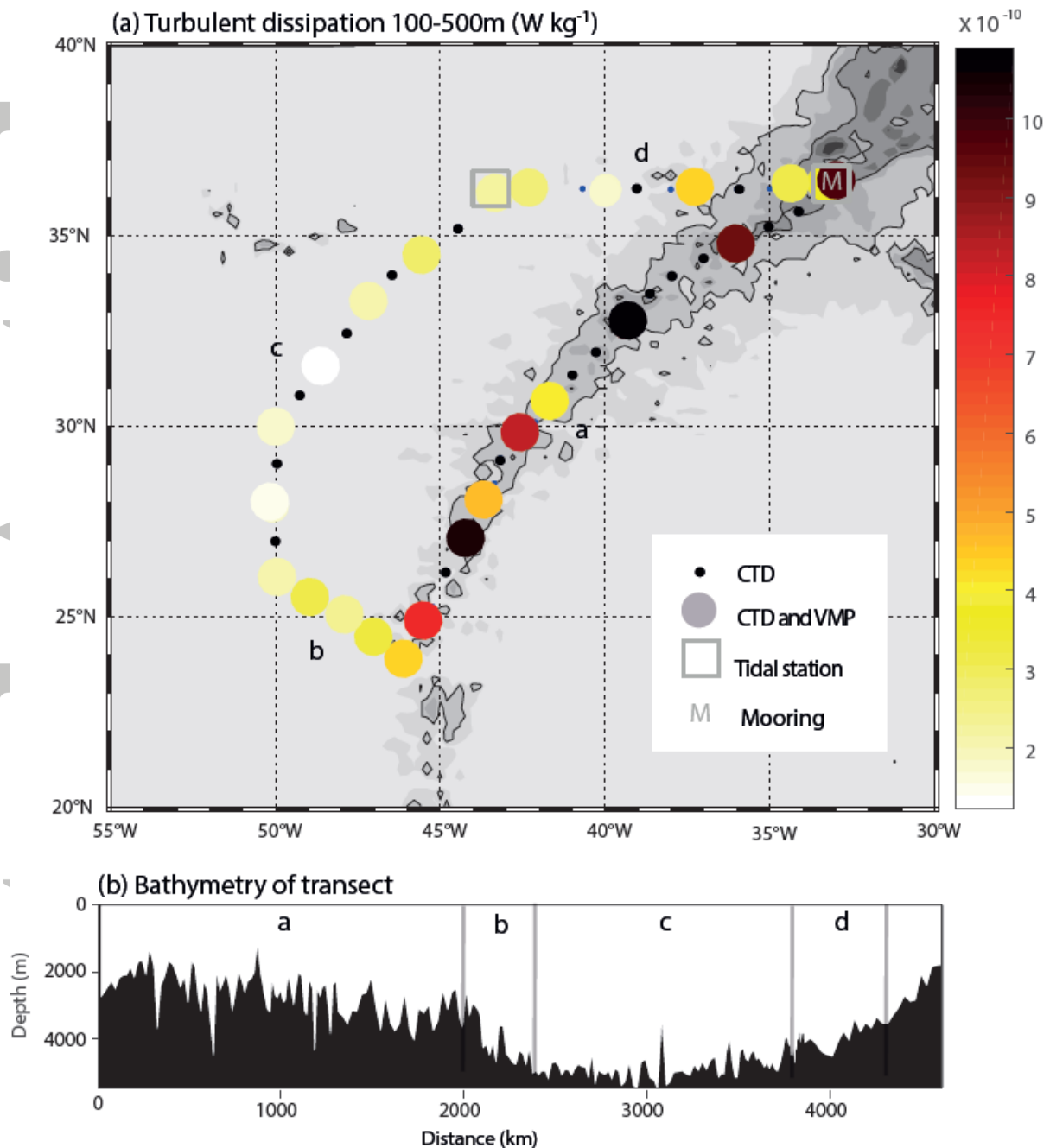
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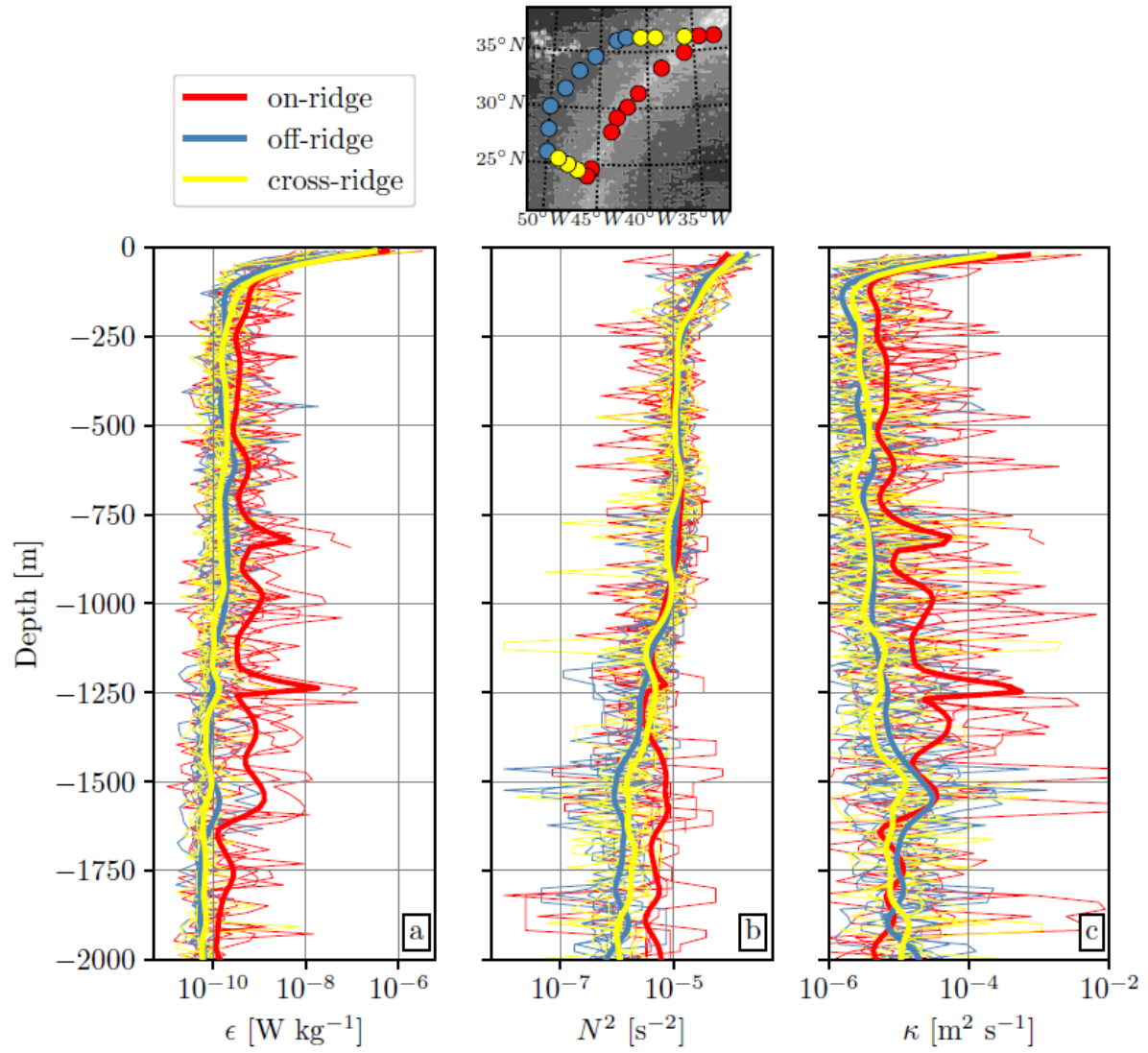


**Table 1. Variation in diapycnal diffusivity and diapycnal nutrient fluxes at the DCM over time and space scales.** (a) The mean diffusivity at the base of the DCM (using a depth range between the depth of the DCM and the depth at which chlorophyll drops to 10% of the peak chlorophyll) from each profile was used to compute the zonally-averaged diffusivity on and off ridge and the spring and neap variability at the tidal stations in Figure 1. (b) The estimates of diffusivity in (a) were combined with local nitrate gradients to calculate the diapycnal nitrate supply to the DCM (converted to  $\text{mol N m}^{-2} \text{yr}^{-1}$ ). The ranges in parentheses represent  $2\sigma$ .

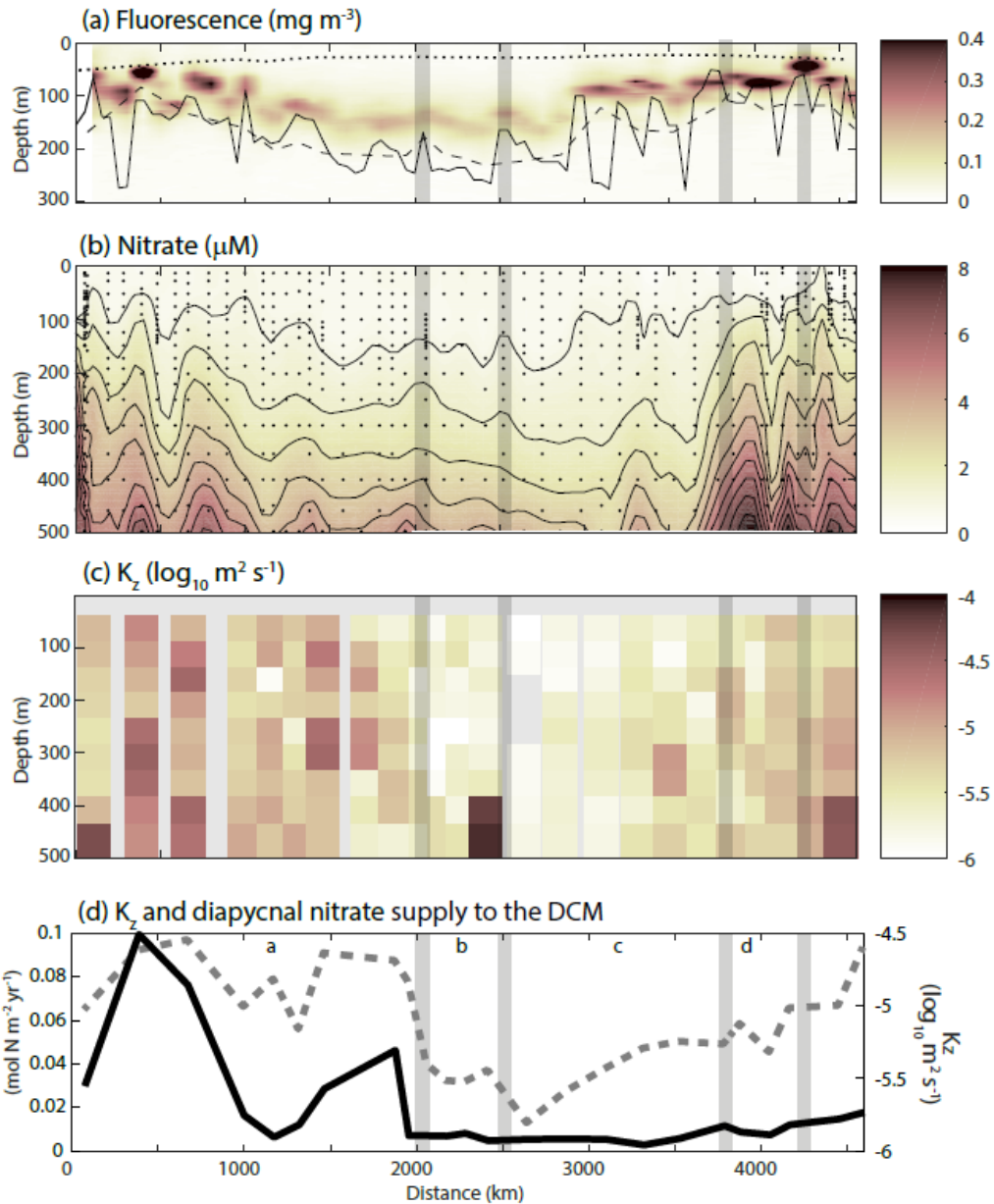
<b>Diffusivity and diapycnal nitrate fluxes at the deep chlorophyll maximum</b>		
<b>(a) Diapycnal diffusivity</b> ( $\text{m}^2 \text{s}^{-1}$ )	On ridge	$1.3 \times 10^{-5}$ ( $0.5\text{-}1.8 \times 10^{-5}$ )
	Off ridge	$2.3 \times 10^{-6}$ ( $1.3\text{-}3.4 \times 10^{-6}$ )
	Spring (on ridge)	$9.3 \times 10^{-5}$ ( $2.2\text{-}16.4 \times 10^{-5}$ )
	Spring (off ridge)	$4.6 \times 10^{-6}$ ( $2.9\text{-}6.3 \times 10^{-6}$ )
	Neap (On ridge)	$1.3 \times 10^{-5}$ ( $1.0\text{-}1.6 \times 10^{-5}$ )
<b>(b) Diapycnal nitrate supply</b> ( $\text{mol N m}^{-2} \text{yr}^{-1}$ )	On ridge	0.030 (0.009-0.058)
	Off ridge	0.002 (0-0.005)
	Spring (on ridge)	0.271 (0.017-1.030)
	Spring (off ridge)	0.004 (0.002-0.007)
	Neap (On ridge)	0.032 (0.010-0.062)



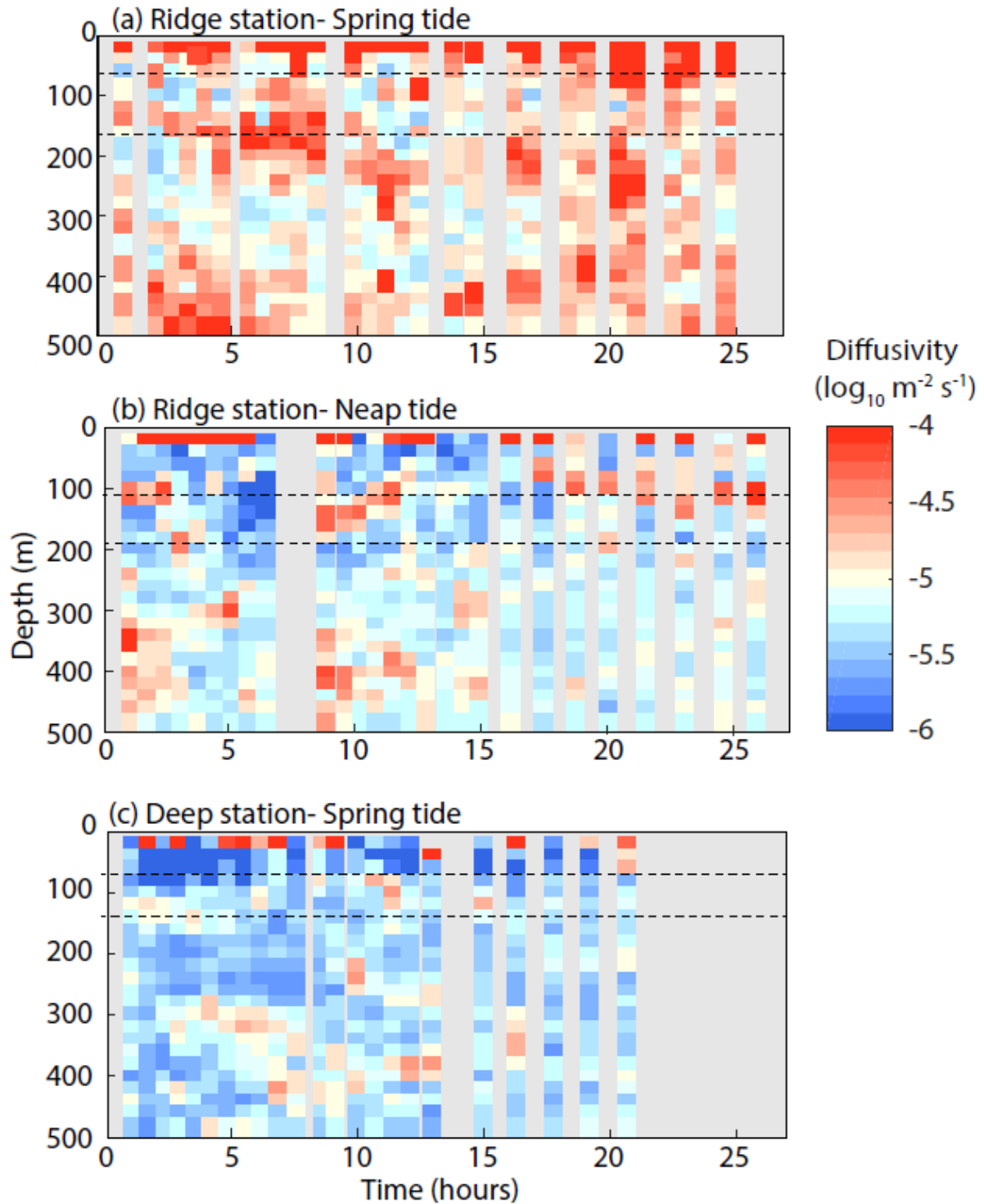
**Figure 1.** (a) Map of study area displaying locations of full water column CTD (conductivity, temperature, depth) and Vertical Microstructure Profiler sampling over the Mid-Atlantic Ridge and in the adjacent abyssal ocean. Filled circles indicate the average water column turbulent kinetic energy dissipation between 100-500m, which are enhanced along the ridge (eastern transect). The on and off ridge tidal stations and mooring are highlighted in the northern transect. (b) The changing bathymetry plotted against distance along the cruise track, the on-ridge, a, off-ridge, d, and cross ridge, b, d, sections are highlighted.



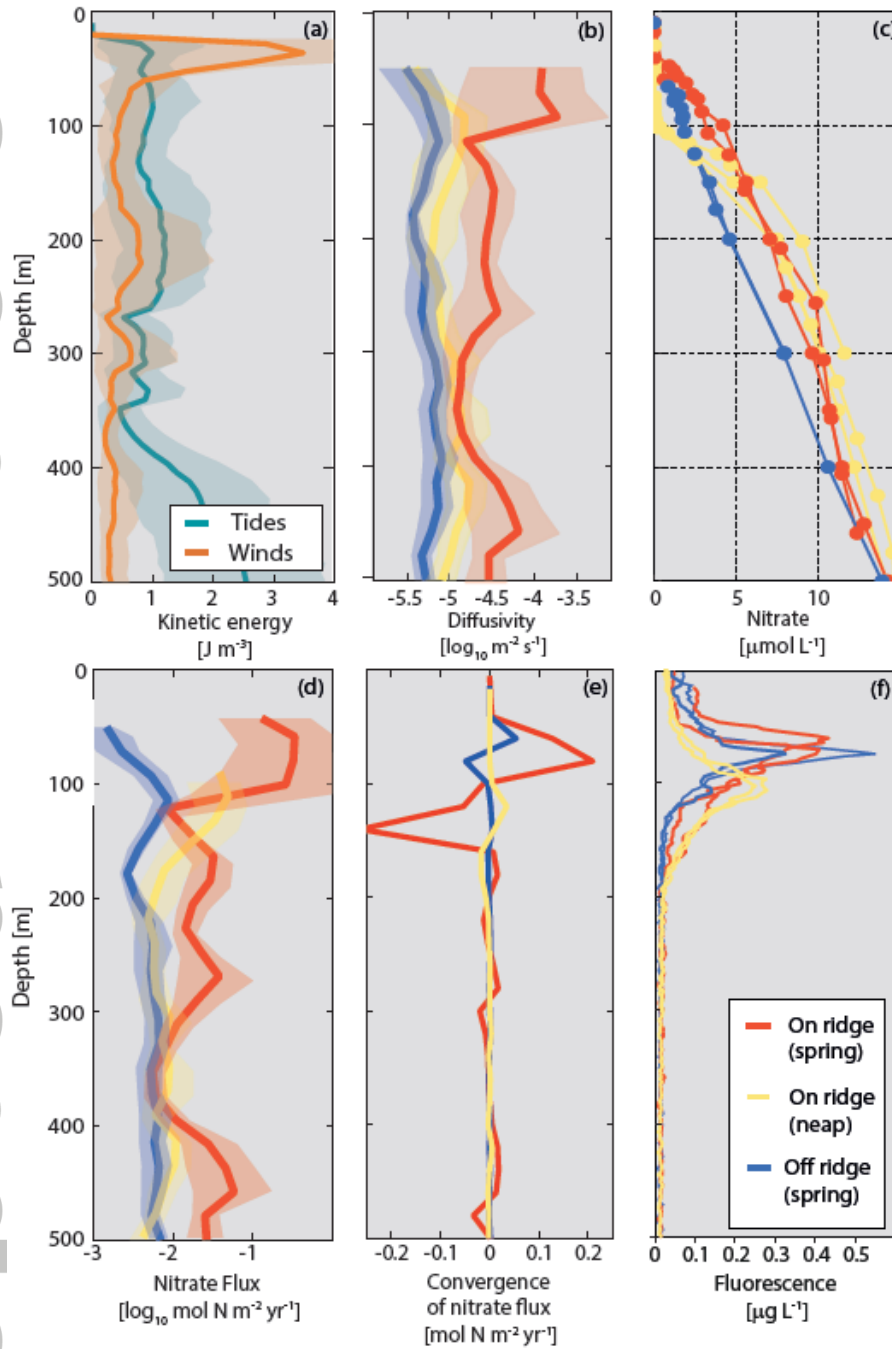
**Figure 2.** Depth profiles of (a) turbulent dissipation ( $\text{W Kg}^{-1}$ ), (b)  $N^2$  ( $\text{s}^{-2}$ ) and (c) turbulent diffusivity ( $\text{m}^2 \text{s}^{-1}$ ) in the upper 2000 m across our study site. Stations are defined either as on-ridge (red), cross-ridge (yellow) and off-ridge (blue).



**Figure 3.** Along track changes in chlorophyll, nitrate and  $K_z$ . (a) Fluorescence ( $\text{mg m}^{-3}$ ) in the upper 300m with the warmest colours indicating the DCM. The solid line shows the depth of the maximum nitrate gradient, the dashed line shows the depth at which chlorophyll decreases to 10% of its maximum and the dotted line shows the depth of the mixed layer (b) Nitrate concentrations ( $\mu\text{M}$ ) in the upper 500m against distance along cruise track. (c) Vertical diffusivity,  $K_z$  ( $\log_{10} \text{m}^2 \text{s}^{-1}$ ), in the upper 500m as measured by the vertical microstructure profiler. (d) Mean diffusivity,  $K_z$  (dashed line) and estimated diapycnal nitrate supply to the DCM (solid line). Nitrate supply to the DCM was calculated from the convergence of the nitrate flux (nitrate gradient ( $\text{mmol m}^{-4}$ ) multiplied by the diffusivity,  $K_z$  ( $\text{m}^2 \text{s}^{-1}$ )), between the peak of the DCM and the depth at which chlorophyll drops to 10% the maximum chlorophyll concentration. Grey lines separate on-ridge, off-ridge and cross-ridge sections labelled in Figure 1.

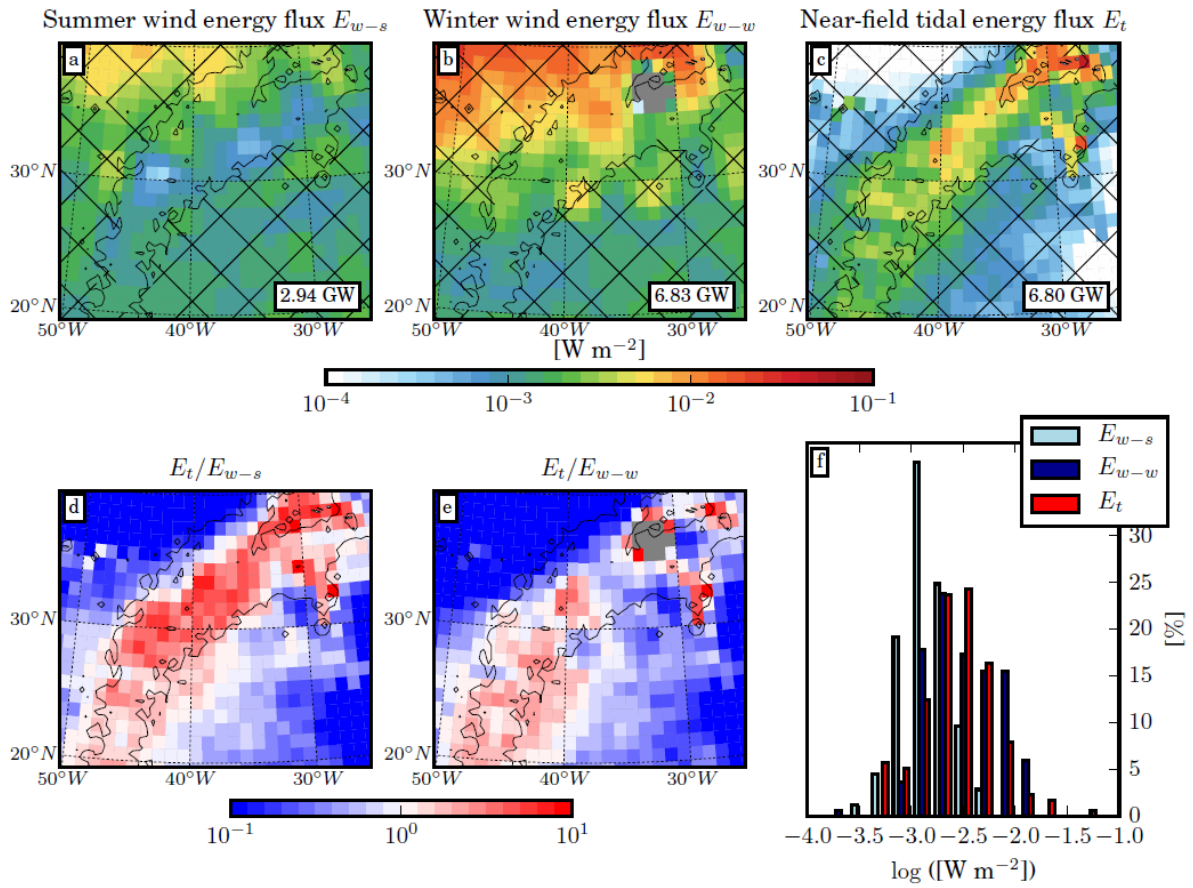


**Figure 4.** Tidal variation in vertical diffusivity at the on ridge and off ridge stations over 25 hour periods in the upper 500m. (a) On ridge station during the spring tide, (b) On ridge station during the neap tide, and (c) Off ridge station during the spring tide ( $\log_{10} \text{ m}^{-2} \text{ s}^{-1}$ ). The dashed lines on each plot represent the depth interval used to calculate nutrient fluxes in Figure 5, from the DCM to where fluorescence decreases to 10% of its maximum.

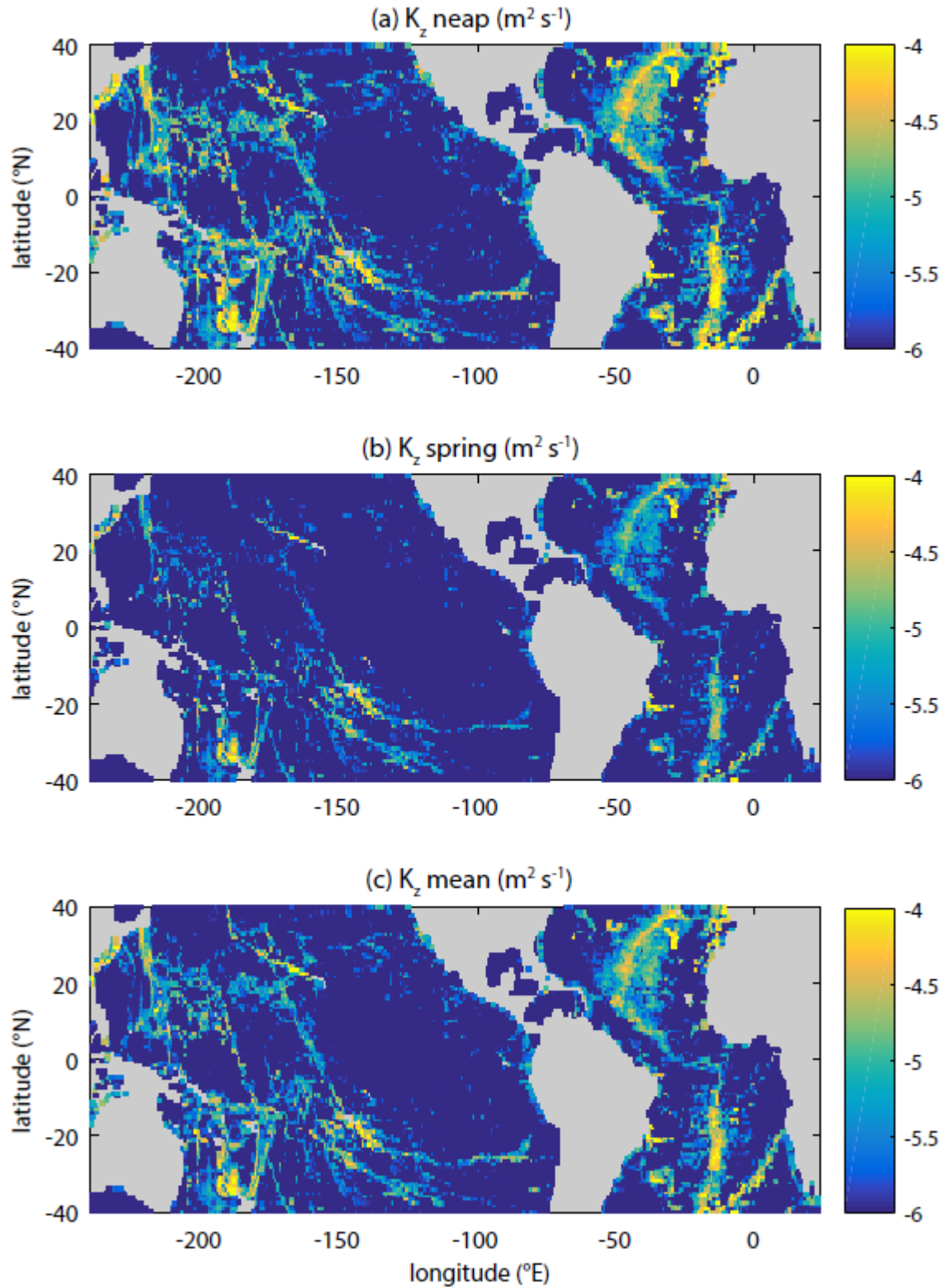


**Figure 5.** (a) Mean ( $\pm 1\sigma$ ) profiles of kinetic energy per unit volume ( $\text{J m}^{-3}$ ) for semidiurnal (blue) and near-inertial frequencies (orange), where semidiurnal signal is viewed as from the M2 tides and the near-inertial signal from the winds; computed from velocities from the ADCP mooring (located at the on-ridge tidal sampling site). (b) Bootstrapped average and 95% confidence limits of diffusivity in the upper 500m ( $\log_{10} \text{m}^2 \text{s}^{-1}$ ), (c) Vertical nitrate profiles ( $\mu\text{mol L}^{-1}$ ), (d) the implied diapycnal nitrate fluxes ( $\log_{10} \text{mol N m}^{-2} \text{yr}^{-1}$ ) using the nitrate gradient ( $\text{mmol m}^{-4}$ ), (e) local convergence of nitrate flux ( $\text{mol N m}^{-2} \text{yr}^{-1}$ ), positive indicates supply of nitrate, negative indicates loss of nitrate, (f) fluorescence profiles from the CTD which were used to calculate the nitrate gradient (the depth range between the DCM and where the DCM decreases to 10% of its maximum).

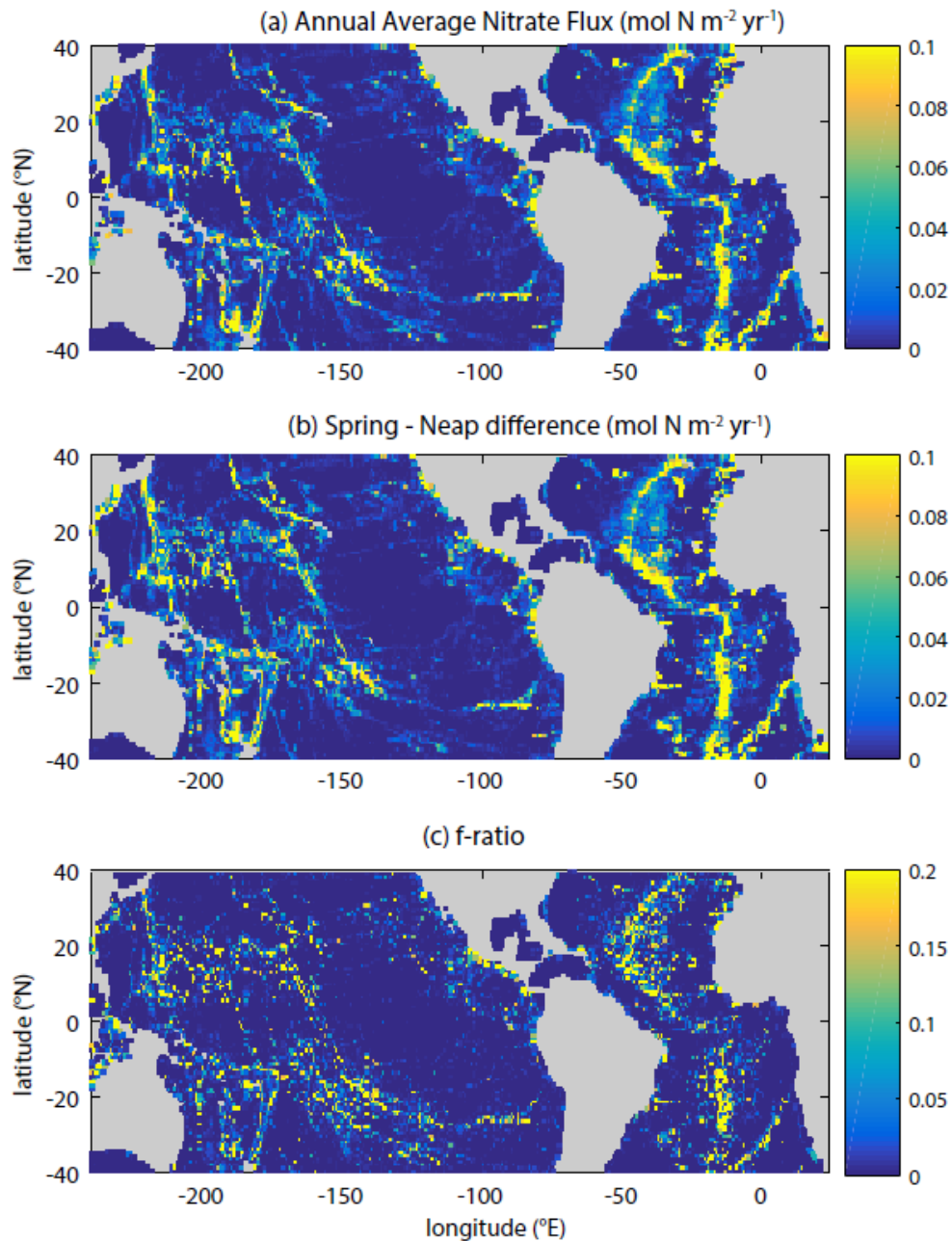




**Figure 6.** Regional estimates of near-field tidal and wind energy fluxes. (a) winter wind energy flux,  $E_{w-w}$ , (b) summer wind energy flux,  $E_{w-s}$ , and (c) tidal energy flux,  $E_t$ , in  $\text{W m}^{-2}$ , including 2000 m and 4000 m bathymetry (black contours), together with (d) ratio of the tidal energy flux / summer wind energy flux, (e) ratio of the tidal energy flux / winter wind energy flux, and (f) histogram of the three energy fluxes over the mid-Atlantic ridge, (hatch-free area in panels (a),(b),(c)), defined by latitude 20-38°N, longitude 25-50°W and bathymetry <4000 m. Integrated energy fluxes over the domain are given in panels (a), (b), (c) in GW.



**Figure 7.** Spring and neap tidal variations in upper ocean diapycnal diffusivity  $K_z$  (100-500m). Upper ocean  $K_z$  ( $\log_{10} \text{m}^2 \text{s}^{-1}$ ) is calculated at spring and neap tides over the low latitude ocean, (a)  $K_z$  over neap tides, (b)  $K_z$  over spring tides and (c) tidally-averaged  $K_z$ .



**Figure 8.** Estimated tidal variation in diapycnal nitrate fluxes over the Atlantic and Pacific basins between 40°S and 40°N. Nutrient gradients were estimated using the maximum gradient in the upper 500 m from WOA climatology. Diapycnal diffusivity was calculated using dissipation from the TPOX8 database assuming that the energy redistributed in the vertical is directly proportional to the buoyancy frequency. (a) Annual average diapycnal nitrate flux in  $\text{mol N m}^{-2} \text{yr}^{-1}$ . (b) Tidal variability (spring tide minus neap tide) in  $\text{mol N m}^{-2} \text{yr}^{-1}$ . (c) Estimated f-ratio at the DCM. Calculated by assuming the nitrate flux is converted to carbon fixation following Redfield stoichiometry ( $\text{C:N}=106:16$ ) and the calculated f-ratio =  $[\text{Redfield C fixed by internal tidal supply of N}] / [\text{annual net primary production from satellite}]$ , annual net primary production is calculated using published methods (Behrenfeld et al., 2006).